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**Abstract:** Human language has particular unusual structural properties that enable open-ended communication. In recent years, researchers have begun to appeal to cultural evolution to explain the emergence of these structural properties. A particularly fruitful approach to this kind of explanation has been the use of laboratory experiments. These typically involve participants learning and interacting using artificially constructed communication systems. By observing the evolution of these systems in the lab, researchers have been able to build a bridge between individual cognition and population-wide emergent structure. We review these advances, and show how cultural evolution has been used to explain the origins of structure in linguistic signals, and in the mapping between signals and meanings.

## Highlights

Key design features of language can be explained as the result of cultural evolution.

Experiments have found that structure emerges through transmission and communication.

Cultural transmission leads to compressible representations.

Communicative use leads to expressive languages.

# The Cultural Evolution of Language

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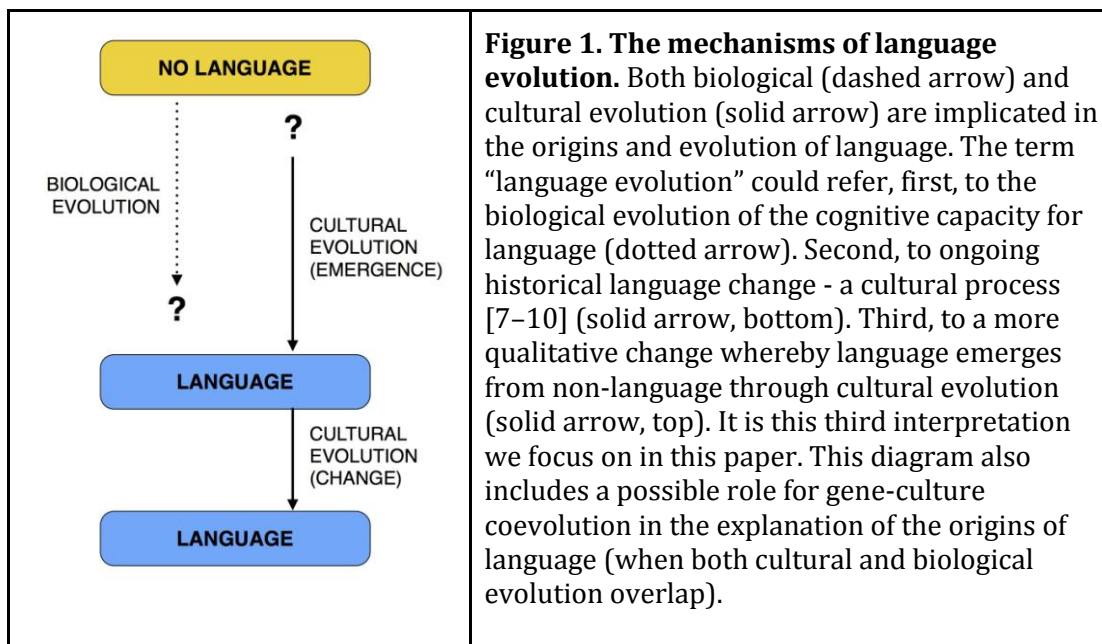
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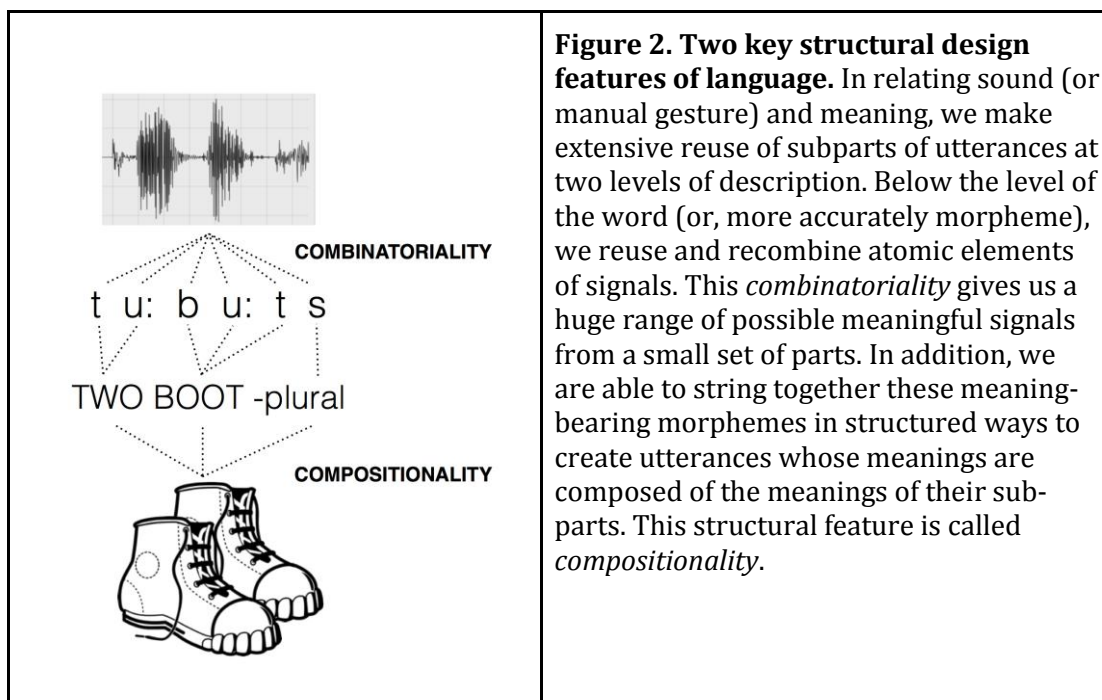
Human language has unusual structural properties that enable open-ended communication. In recent years, researchers have begun to appeal to cultural evolution to explain the emergence of these structural properties. A particularly fruitful approach to this kind of explanation has been the use of laboratory experiments. These typically involve participants learning and interacting using artificially constructed communication systems. By observing the evolution of these systems in the lab, researchers have been able to build a bridge between individual cognition and population-wide emergent structure. We review these advances, and show how cultural evolution has been used to explain the origins of structure in linguistic signals, and in the mapping between signals and meanings.

## Introduction

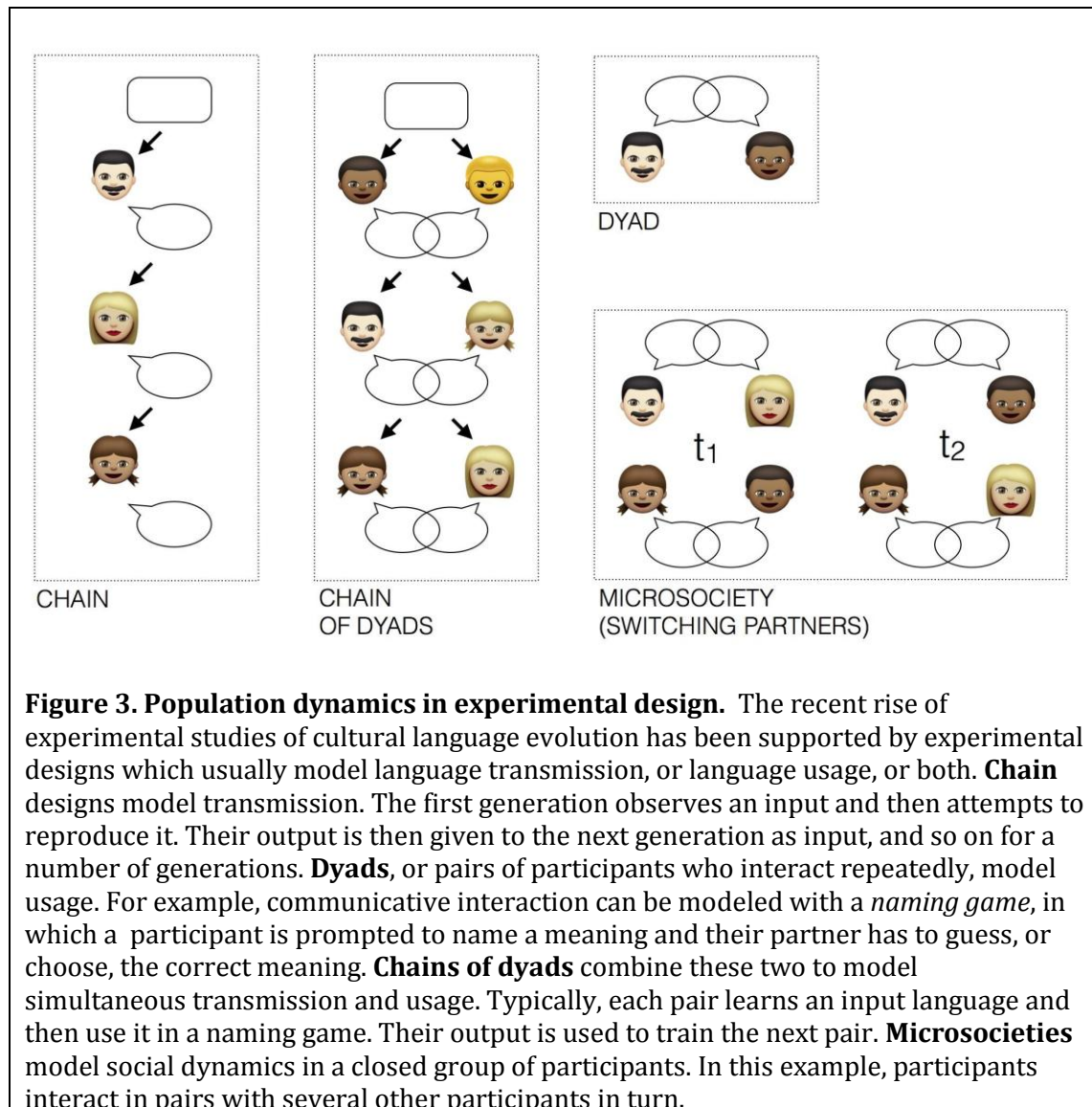
Language is arguably the defining characteristic of our species, and the evolution of language is an area of intense interdisciplinary interest [1–6]. The term 'language evolution', however, has three common interpretations: biological evolution, language change, and the cultural emergence of linguistic structure (Figure 1). This review will focus on the third interpretation. We will examine research looking at whether the way language is transmitted and used can explain the origins and evolution of key design features of language. These are the features which mark language out as special when compared to the vast number of communication systems in the natural world, and enable us to communicate about an open-ended range of meanings.



Transmission to new learners, communicative use, interactions among speakers in a community, and the structure of the world, all leave their imprint on the structure of languages. (See Figure 2 for a description of two structural design features of language that have been claimed to be adaptations arising from cultural evolution: combinatoriality and compositionality). The headline conclusion so far is that language evolves to maximize expressivity under pressures for communication whilst minimizing complexity under pressure to be learnable. Evidence in support of this conclusion comes from experiments [11], computational and mathematical models [12] and data from a wide range of languages [13].



We will focus in this review on experimental approaches to cultural evolution as they have been applied to language (table 1). There is a long history of using transmission chain experiments to look at how behaviour evolves culturally [14–18, see also Whiten, Caldwell, & Mesoudi, this volume]. Kirby et al. [19] emphasise the applicability of this method to language, which they argue undergoes a process they call *iterated learning* [20–23], emphasising the way in which individuals learn from other learners during transmission and usage. Figure 3 gives various different ways in which iterated learning of language has been explored experimentally.



**Figure 3. Population dynamics in experimental design.** The recent rise of experimental studies of cultural language evolution has been supported by experimental designs which usually model language transmission, or language usage, or both. **Chain** designs model transmission. The first generation observes an input and then attempts to reproduce it. Their output is then given to the next generation as input, and so on for a number of generations. **Dyads**, or pairs of participants who interact repeatedly, model usage. For example, communicative interaction can be modeled with a *naming game*, in which a participant is prompted to name a meaning and their partner has to guess, or choose, the correct meaning. **Chains of dyads** combine these two to model simultaneous transmission and usage. Typically, each pair learns an input language and then use it in a naming game. Their output is used to train the next pair. **Microsocieties** model social dynamics in a closed group of participants. In this example, participants interact in pairs with several other participants in turn.

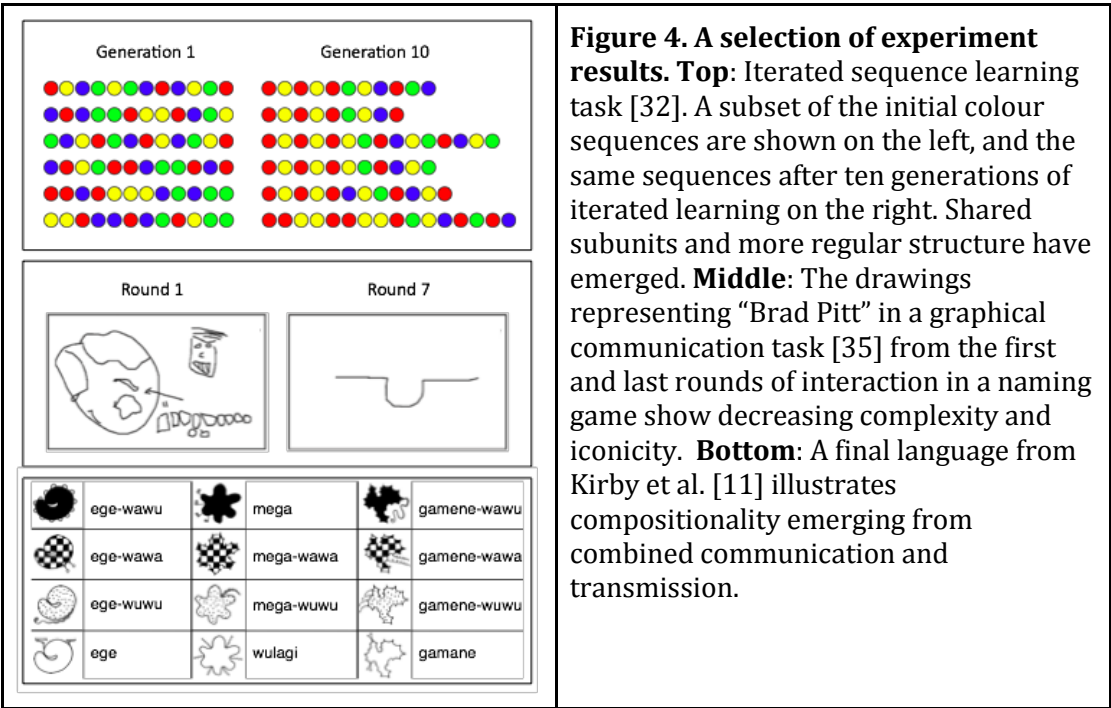
## Signals

Why is human language combinatorial (Figure 2)? One answer might be that it arises in response to the need for a large vocabulary. Hockett [24] argues that once a system has too many meanings to be efficiently encoded by distinct non-combinatorial forms, a combinatorial system becomes advantageous. More recently, an alternative hypothesis has been proposed [25] that combinatoriality emerges through cultural transmission under biases favouring simplicity. In Verhoef's [25,26] cultural transmission

experiments inspired by earlier simulation work (e.g., [27–31]), participants had to learn and reproduce a set of twelve distinct, independent slide-whistle sounds. Their produced sounds became the set the next participant had to reproduce, creating a transmission chain (Figure 3). At the end of ten generations, the whistle sounds had become easier to reproduce. They had ceased to be independent; many of them shared discrete internal elements, despite the continuous nature of the slide-whistle medium. In other words, they had developed combinatorial structure.

In related work, Cornish et al.’s [32] transmission chain experiment explored the extent to which cultural evolution can explain the origins of systematic structure in sequences of discrete rather than continuous signals. Their participants had to observe and then recall a large number of sequences of flashing lights. Over ten generations, the sequences became increasingly accurately reproduced, and the set of sequences began to show systematic structure (see Figure 4). Subsequences came to be reused and recombined across different items in the set, and incipient hierarchical structure emerged towards the end of the chains.

These examples illustrate the evolution of *compressibility* of the behaviours of the participants over generations. In both studies, the sets of behaviours have lower entropy at the end of the chains than they did at the start. Entropy is a measure of the amount of information in a sequence; low entropy sequences can in principle be compressed because they contain inherent redundancies. Redundancies allow us to construct short descriptions of behaviour. For example, grammars are concise descriptions of linguistic behaviour that can be constructed precisely because language contains systematic, compressible regularities. This emergence of compressibility in behaviours has been argued to be a characteristic outcome of iterated learning [11]. The generality of this outcome has also been demonstrated experimentally in non-linguistic tasks [33,34].



### Mappings between signals and meanings

Linguistic signals fulfill their communicative function because they have conventionally associated meanings which are shared by a community of speakers. A number of

experiments have explored how signal-meaning mappings come to be shared (however, see [6] for the limitations of treating languages as mappings). Fay et al. [35] used a graphical communication design in which a microsocociety of participants (Figure 3) played naming games based on a 'pictionary' task: a participant had to draw a signal to communicate a meaning to his or her partner. Initially, individuals had different variant drawings for the same meaning, but over interactions with several partners, the population tended to converge on the same variant. Fay et al. [35] thus showed how local, pairwise interactions lead to the emergence of global conventions (see also simulations of microsocieties, e.g. [36]).

As the signal-meaning mappings spread, they were affected by the cultural equivalent of natural selection. Participants preferentially adopted signal variants whose intrinsic properties made them easier to learn, and they also tended to reproduce their own variants more than those produced by their partners [37]. In addition, when the experimenters reduced the number of participants in a microsocociety, the signals that arose were more difficult to reproduce and their meaning was less transparent for naive observers relative to the ones produced by larger groups of participants. In other words, they changed from being *iconic* – where the form resembles the meaning – to being *symbolic* – where form and meaning are related by an arbitrary convention (Figure 4) [38]. At the same time, this process of transparency loss, driven by conventionalization, favoured the emergence of combinatoriality [39].

Another widespread feature of language is that the mapping between signals and meanings tends to be *regular*. For example, we tend not to have many synonymous words for the same meaning. This can also be seen as reflecting a preference for compressibility because systems with unconditioned variation have higher entropy. Could this too be a result of cultural evolution? Smith & Wonnacott [40] addressed this question by implementing a transmission chain in which participants first learned to relate various pictures with labels from an artificial language, and then attempted to reproduce these labels when prompted by pictures. They started their experiment with a language with unpredictable variation in signals. Over generations, this unpredictable variation came to be regularised. Previously, it was thought that regularisation was a result of children's particularly strong bias for regularisation [41], but Smith & Wonnacott's [40] participants were adults, showing that cultural evolution can act to amplify weak biases over generations. Other studies [42,43] have shown that the bias for regularisation may be modulated by task domain, suggesting that the pressure to regularise may be particularly strong in language tasks. In addition, regularisation has been used as a tool to investigate the origins of universal asymmetries in word order across languages; by presenting participants with variable word order and examining the particular way they regularise, Culbertson et al. [44] relate individual learning bias and language universals (see also [45,46] for an alternative approach to word order universals using improvised gestural communication).

Kirby et al [19] also look at the effects of cultural transmission on signal-meaning mappings using a transmission chain design, building on closely related modelling work (see, e.g., [12] for review). However, rather than focus on variability in the way a meaning might be produced, they wanted to see if compositionality (Figure 2) could emerge from a situation with initial one-to-one mappings. However, in their first experiment, they found languages evolving in which multiple meanings mapped to the same signal. In other words, the languages became easier to learn but at the expense of *expressivity*. In a later paper, Kirby et al [11] suggest that language is both learnable and expressive because it is being shaped by two pressures: communication and transmission. Accordingly, they added a communication task to the design by using a chain of interacting dyads rather than single individuals (Figure 3). The result was a



language that optimised both compressibility and expressivity. The solution that the evolving language found was to exhibit compositionality: parts of the signals mapped on to parts of the meaning (Figure 4). Converging evidence that language does indeed trade off compressibility and expressivity comes from cross-linguistic studies of semantic categories across a wide range of domains [13], including numerals [47], colour [48], spatial [49], and kinship [50] terms.

The structure of the mapping between signals and meanings is influenced by the structure of meanings themselves [51]. Roberts et al [52] had dyads of participants (Figure 3) convey meanings that were either easy or hard to represent iconically in a graphical medium (animal silhouettes and shades of green, respectively). The signals that evolved after repeated communicative interactions differed structurally across conditions: many unique, distinct complex signals evolved for the animals, while a combinatorial system that used a smaller set of simpler signals evolved for the shades of green.

Language structure adapts not only to the underlying structure of meanings, but also to whether a meaning distinction is relevant for communication or not. Distinctions that are frequently relevant for disambiguating meaning in context are more likely to become encoded in the language in the form of distinct labels [53,54].

**Table 1**

Modelling the cultural evolution of language: a map of the main parameters to explore with a selection of example references.

Type of information transmitted	Participant task	Population dynamics	Structure of meaning space	Dependent variables
Meaning categories [53,55]	Reproduction [11,19,25,26,33,40,42,43,51,53]	Transmission chains [19,32-34,40,43,51,53]	Single item [33,34]	Reproduction accuracy [11,19,25,26,32,35,39,51]
Linguistic signals [11,19,51,53,54,56]	Naming games [11,35,39,52,54,56,58]	Dyads [11,39,52,56,57]	Multiple independent items [32,35,52]	Complexity [32,33-35,58,62]
Frequency distributions [40,42,43]	Other communication games [57,61]	Microsociety [35]	Multiple discrete dimensions [11,19,40,53,54,57,64]	Combinatoriality [25,26,39]
Non-linguistic (visual) [33-35,53,57-59]		Transmission chains of dyads [11,54]	Frequency-structured [40,42,43]	Compositionality [11,19,64]
Non-linguistic (auditory) [25,26,60]		Replacement [62]		Regularity (entropy) [40,42]
Gestural [45,46]		Self training [63]	Continuous [51]	Identification accuracy [38,39,62]
				Iconicity [39,52]

## Conclusions and future directions

Linguistic structure evolves culturally under pressure from learning and communication. Languages adapt to the first pressure by becoming compressible; to the second, by maintaining relevant distinctions. Both together lead inevitably to the characteristic structural design features of language such as combinatoriality and compositionality.

We have focussed in this review on cultural evolution as it applies to the emergence of fundamental features of language. However, returning to Figure 1, we are left with an open question about the role of gene/culture coevolution in the evolution of language (see, e.g. [65–70], for discussion). We have also implicitly emphasised human uniqueness in this review, but it is worth noting that there have been recent attempts to explore this kind of cultural evolution of systems of behaviour from a comparative perspective (see, [59] for an experiment with baboons, and [60] et al for one with zebra finches.).

Much of the work in language evolution that we have summarised here focuses on the explanation of fundamental design features of language. However, linguists have also identified so-called "language universals" - universal constraints and tendencies in the distribution of linguistic variation. An area of particular interest concerns the ordering the words in a sentence. Some orders are more frequently attested across languages than others [71]. For example, languages which place the adjective after the noun, rather than before (as in English), are more common than would be expected by chance. [72–74] have pioneered an experimental approach to explaining word order patterns using techniques from artificial language learning or so-called "silent gesture" experiments. These experiments test whether individual participants' biases reflect the distribution of orders we see in the world's languages. A critical direction for future work would be to integrate this approach with a cultural evolutionary perspective. For example, an obvious extension would be to embed the silent gesture method within a diffusion chain experimental design. In this way, we could extend the remit of cultural evolutionary studies of language beyond design features to take in a wide variety of phenomena of interest to linguists.

Ultimately, a truly explanatory account of human language needs to take into account the fact that language is the result of particular cognitive adaptations; that these cognitive adaptations enable and shape the cultural transmission of language; and whatever emerges from the process of cultural evolution will itself alter the selection pressures operating on human evolution.

\*\* [11] Using experiments and Bayesian modelling, the authors show that compositional structure emerges as a compromise between compressibility and expressivity. The former is the result of a pressure on language to be learnable, whereas the latter arises from a pressure to be communicatively useful.

\*\* [40] This transmission chain experiment shows that, over multiple generations of learners, unpredictable variation in languages is regularized. Starting with a language in which meanings are expressed with free variation, a system emerged in which this variation was entirely conditioned on meaning distinctions.

\*\* [35] This study of the spread of communicative signal variants in a population playing a graphical communication game shows that local interactions result in a global coordinated system; as they evolve, the signals also change by losing complexity and iconicity.

\*\*[57] In this pioneering study, pairs of participants had to create a novel communication system to tell each other about their location using an unfamiliar communication channel. The emerging signals were adapted to the limitations of the channel and to the structure of the geographical environment.

\* [51] This paper demonstrates the importance of structure in the world on the structure of languages that evolve through iterated learning. The authors manipulate a continuous meaning space in an experiment so that certain features are highlighted, leading to these dimensions being preferentially expressed.

\* [26] In order to model the emergence of phonological combinatoriality, the authors in this study implement a transmission chain in which participants copy slide-whistle patterns. From an initially continuous signal space, combinatorial structure emerges such that the final set of signals is made up of discrete recombinable elements.

\* [37] This study quantified selection biases acting on the spread of communicative variants in a population communicating using drawings. The authors found that variants were transmitted with high fidelity, but also showed the unequivocal effects of content and egocentric selection biases.

\* [19] This was the first cultural evolution experiment to look at how compositional structure might emerge through iterated learning alone. The authors found that compositionality required both cultural transmission, and some additional pressure for expressivity.

\*[53] Using an iterated learning paradigm, the authors show that the context of communication - i.e. which particular meanings need to be discriminated at the point where an utterance is produced - matters for the structure of the evolving language. Features that do not need to be discriminated end up not being expressed in the language.

\* [55] In this transmission chain study, participants have to reproduce new ways to categorize the meaning space of colours. The categories that emerge after several generations in different chains all reflect human learning and perceptual biases, and mirror the types of language we see in the world.

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